Gentlemen first? 'Broken stick' modeling reveals sex-related homing decision date in migrating seabirds

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Running title: Homing decision date in penguins

Abstract

Technical progress in animal-borne tracking and movement data analysis has facilitated understanding the interplay between successive periods in the life-cycle of migratory animals. We investigated how sex differences on the constraints of homing may influence migration to breeding areas in crested penguins (genus *Eudyptes*). We used a novel approach to infer homing decision-date, a precise point in time which translates statistically as a change-point in the current distance of the animal to its colony ('broken stick' modeling approach, R codes provided here). We applied this approach to geolocation tracking data on migration in three *Eudyptes* species, from three localities in the southern Indian Ocean (5 populations). Sex had a subtle and consistent influence on the temporal activity of the 66 animals during their migratory journey. Males began migration to the breeding localities earlier than females, by an average of 9.1 (range: 4.5–13.5) d. This difference was statistically significant in 4 of 5 populations, and occurred among all species, sites and years surveyed. Our study shows an original application of a recent modeling approach to detect change-point in movement data. Our results suggest that sex-specific constraints related to breeding in migrating animals may also modify activity schedules well before breeding commences.

Keywords: migration, pre-breeding period, broken stick modeling, *Eudyptes* penguins, sex-specific constraints, activity schedule, light-based geolocation, temporal resource

Introduction

Understanding the interplay between successive periods of the life-cycle in migratory animals has long been constrained by our inability to track individuals across different phases (Sorensen *et al.*, 2009). To track migrating animals' movements over their complete non-breeding phase is difficult indeed, especially marine species such as seabirds, which are generally inaccessible when not breeding (Hamer, Schreiber & Burger, 2002). Consequently, our knowledge about their non-breeding phase has long remained poor (Warham, 1975; Stahl *et al.*, 1985; Williams, 1995). However, over last two decades both animal-borne tracking and movement data analysis techniques have considerably improved and unraveling the behavioural adjustments taking place at sea may now be feasible (Wilson & Vandenabeele, 2012).

In this study we therefore used some of the latest developments in both tracking and data analysis to investigate how the sex-specific adjustments on arrival date in their upcoming breeding season may affect migration patterns in penguins. We focused on the crested penguins (genus *Eudyptes*). This is the most diverse penguin genus, and their complete non-breeding phase whilst at sea is now well described for several species, thanks almost exclusively to the use of recently developed, ultra-miniaturized light-based geolocation loggers (GLSs).

Penguins are very sensitive to instrumentation (Bannasch, Wilson & Culik, 1994), which precludes the use of large archival tags for extended periods at sea for both technical and ethical reasons. However, the size, shape and logging capacity of GLSs allowed us to collect data during their entire period of 5–7 months at sea, without major ethical considerations.

Eudyptid penguins can venture thousands of km from their colonies to reach their wintering areas, travelling ~50 km per day (see Bost *et al.*, 2009; Thiebot *et al.*, 2011, 2012). Among studies on crested penguin species over the non-breeding season, no significant sex

69 differences in foraging areas have been reported (Pütz *et al.*, 2002, 2006; Raya Rey, Trathan
70 & Schiavini, 2007; Bost *et al.*, 2009; Thiebot *et al.*, 2011, 2012). Yet, male *Eudyptes*
71 penguins typically arrive at the colony *c.* 1 week prior to females in order to occupy nesting
72 places (Warham, 1975; Williams, 1995). It is unknown whether this difference in arrival date
73 between sexes is due to the fact that males may leave their offshore wintering site and start
74 their pre-breeding migration earlier than females. Alternatively, both sexes may leave the
75 wintering area concurrently, but that males travel faster than females, or that females remain
76 at-sea near the shore while males occupy their nests, remains to be measured.
77 To identify the date when male and female penguin started to migrate back from their
78 wintering site to their breeding site (the "homing decision date"), we relied on an innovative
79 'broken stick' modelling method. A method for unambiguously and clearly identifying this
80 event is necessary because: (1) light-based geolocation precludes direct inference of homing
81 date from visual inspection of the location estimates due to their low spatial accuracy; (2)
82 inference from the single farthest location may lack support from objective criteria of general
83 animal movement and (3) in seasonal environments migration activity may coincide with
84 solar cues such as the equinox (Hamer, Schreiber & Burger, 2002), a period when latitude
85 estimation is unreliable (Wilson *et al.*, 1992; Hill, 1994). Our underlying hypothesis was that
86 contrasts between sexes in arrival date for breeding may be reflected in shifts in pre-breeding
87 migration timing. We applied the modeling method to a previously acquired large dataset on
88 the complete migration in three *Eudyptes* species, the macaroni *E. chrysolophus*, the eastern
89 rockhopper *E. filholi* and the northern rockhopper *E. moseleyi* penguins, from three localities
90 in the southern Indian Ocean (Bost *et al.*, 2009; Thiebot *et al.*, 2011, 2012).
91

Materials and methods

Datasets were collected at three localities in the southern Indian Ocean: Crozet (46°24'S, 51°45'E), Kerguelen (49°20'S, 69°20'E) and Amsterdam (37°50'S, 77°31'E) islands. Penguins were equipped with leg-mounted miniaturized light-based geolocation loggers (GLSs, model: BAS MK4, British Antarctic Survey, Cambridge, UK) in 2006 and 2007. These loggers (mass: 6 g) record ambient light level every ten minutes, thus geographic location can be estimated from local day /night duration and sun zenith time (Wilson *et al.*, 1992; Hill, 1994). This light-based geolocation approach allows location to be estimated twice a day, i.e., at mid-day and midnight, with a mean spatial error of tens to hundreds km for diving animals (*c.* 120–130 km on average, Staniland *et al.*, 2012). In addition, these loggers also record ambient sea temperature with a resolution of 0.06°C and an accuracy of ±0.5°C. Temperature records were incorporated in the location estimation process, together with a land mask precluding terrestrial locations and specific movement parameters (mean, variance and distribution of movement speed) for the animals, following a Bayesian approach (Sumner, Wotherspoon & Hindell, 2009; Thiebot & Pinaud, 2010). This approach enabled the determination of the most probable location estimates. In total, 66 individual tracks were collected from the three sites: 12 in 2006 (*E. chrysolophus* from Kerguelen only) and 54 in 2007 (both *E. chrysolophus* and *E. filholi* species on both Crozet and Kerguelen islands, and *E. moseleyi* on Amsterdam, Table 1).

From these tracks we calculated the great-circle distance of each location to the corresponding colony of origin. To infer the dates of change in migration pattern, we used a 'broken stick' modeling approach (e.g. Authier *et al.*, 2012), described below. Specifically, we used the distance to the colony to estimate when birds started to migrate back to their rookeries. This metric was normalized to the interval 0-1 (excluding boundaries) by dividing by the observed maximum distance to the colony for each bird. We analyzed these data with

beta regression (Cribari-Neto & Zeilis, 2010). This regression technique bypasses the need to transform the original data to meet the normality assumption of residuals while intrinsically taking into account the heteroskedasticity and skeweness typical of continuous data ranging from 0 to 1 (Cribari-Neto & Zeilis, 2010). We let $y_{i,t}$ denote the distance ratio of the i^{th} bird on day t:

$$y_{i,t} \sim Beta(\mu_{i,t}, \tau) \quad (1)$$

where $\mu_{i,t}$ is the mean distance ratio:

$$logit(\mu_{i,t}) = \beta_{1,i} + \beta_{2,i} \times Day_{t,} \quad (2)$$

and τ^{-1} is a dispersion (variance) parameter.

We were interested in testing a broken stick-model, where two periods can be distinguished: first a migration away from the breeding colony followed by a return journey to the colony. The break point T_i is the date at which a bird started its back migration (*i.e.*, the homing decision date):

$$logit(\mu_{i,t}) = \beta_{1,i} + \begin{cases} \beta_{2,t} \times (Day_t - T_i), \text{ if Date} \leq T_i \\ \beta_{3,t} \times (Day_t - T_i), \text{ if Date} > T_i \end{cases} \quad (3)$$

To estimate T_i, we used a profile likelihood approach: the likelihood for the model described by the equation above was computed for each location date spanning the inter-breeding period of penguins (see Fig. 1 for an example). The value of T_i that maximized the likelihood was thus evaluated, and an approximate confidence interval for T_i was computed with a Likelihood Ratio Test with 1 df. This method identified a homing decision date for each individual, so we then measured the difference in these dates between males and females in each group or between groups using Student's *t*-test after systematic validation of normality distribution of data with Shapiro-Wilk normality test. In all tests, statistical significance was set at 5%.

142 Computations were performed with the software R (R Development Core Team, 2012)
143 with the *betareg* package (Cribari-Neto & Zeilis, 2010); the *beeswarm* package was also used
144 to draw figures. The R code used is provided as electronic supplementary material with an
145 example to run.
146
147 ## Results
148 For each of the 66 migrating penguins, the broken stick model found a date of change in the
149 individuals' distance to the colony likely reflecting homing decision date (Table 1). The 95%
150 confidence intervals around these dates averaged 6.8 d. Regarding macaroni penguins, at
151 Crozet the date of the change detected was significantly earlier by 8 d in males than in the
152 corresponding females ($t_{8.87} = 2.29$, $P = 0.048$, Fig. 2). On Kerguelen, between two successive
153 years studied the homing decision dates were not significantly different, for each sex (males,
154 2006 2007: $t_{5.46} = 0.30$, $P > 0.7$; females, 2006 versus 2007: $t_{6.91} = 1.49$, $P = 0.2$). Therefore
155 we pooled both years. As for Crozet, males from Kerguelen had a homing decision date that
156 was significantly earlier on average than that of females ($t_{16.64} = 2.60$, $P = 0.019$), with a
157 difference of nearly 12 d observed in both years. In eastern rockhopper penguins, males
158 started their inbound migration significantly earlier (of 4.5 d) than females ($t_{8.44} = 2.44$, $P =$
159 0.039) on Crozet. On Kerguelen the greatest difference between sexes was observed (13.5 d)
160 but was not statistically significant ($t_{5.36} = 1.72$, $P = 0.143$). Finally, male northern rockhopper
161 penguins from Amsterdam started to return back to the colony 5.4 d earlier than females, and
162 this difference was significant ($t_{8.97} = 2.57$, $P = 0.03$).
163
164 ## Discussion
165 Previous colony-based studies have shown that male *Eudyptes* penguins arrive first on the
166 breeding sites; our survey of penguins' at-sea movements before breeding shows that this is

not because they swim faster than females, but because they leave their wintering areas earlier. Sex had a measurable and consistent influence on the onset of migration in each of the three penguin species. Despite unbalanced sample sizes, males consistently started their return to their breeding localities earlier than females by an average of 9.1 (range: 4.5–13.5) d among the 5 groups of penguins. This pattern of earlier homing decision date in males occurred for all three species, on three localities, and for both years surveyed, and hence seems general to the genus.

Male penguins typically exhibit strong territorial activity on their arrival at the breeding site, both when occupying their former nest site and when competing for a new nest site (Williams, 1995). Therefore, competition among males to access prime nesting locations seems a key determinant in the timing of return to the colony as a better nesting site will improve their chances of mating (Warham, 1975; Coulson, 2002). In this context, our results suggest that availability of good nesting locations on the colony would be a limiting factor driving penguins' activity schedule at sea and operating within all three study species.

The approach used here increases the use of GLS dataloggers in seabirds. These devices are increasingly used because they are small enough to be leg-mounted (Bost *et al.*, 2009) and apparently do not modify foraging of diving seabirds (Ropert-Coudert *et al.*, 2009). This is a great advantadge over back-mounted satellite tags, which may have non-negligible impacts (Bannasch, Wilson & Culik, 1994), especially over prolonged periods (Bost *et al.*, 2004). Nevertheless, one drawback of data collected from GLS loggers is their relatively low accuracy in the spatial dimension (Staniland *et al.*, 2012). Here, we show that fine detail in seabirds' behaviour can be obtained from these loggers when considering data in the temporal dimension.

Acquiring these data was only possible because of the fertile cross-polination between cutting-edge techniques: advanced light-based geolocation for prolonged tracking and a novel

use of discontinuous (broken stick) beta regression with movement data. Though no cross-validation with *in-situ* measurements could be carried out, our study on oceanic migrants could objectively determine the homing decision date for each tagged individual. Importantly, this method is better than choosing a single estimate of geographic location. Single estimates may be erroneous due to the low spatial accuracy of each GLS location (especially during vernal and autumnal equinoxes), or because of erratic movements of the tracked animal, whatever the tracking device used. Our approach is therefore preferable because it takes a broader view of the animal's movement, and is not dependent upon a single location. It also suggests that valuable information can be extracted from equinoctial locations, and for this reason that studies should aim at refining them rather than discard them.

Previous use of this modelling technique in behavioural ecology has focussed on estimating change-points for ontogenetic shifts with stable isotope data in seals (Authier *et al.*, 2012). Determining a change-point in biological data is a very broad requirement in ecology and this method is particularly relevant in this context, because it also provides a confidence interval around the estimated value (see also Roth *et al.*, 2012). We recognise that we applied this method in the context of a relatively simple, though fairly general, case of migration: penguins moved relatively directly to their wintering area, and then came back to their colony in a straightforward manner. In the case of animals performing more complex migration schemes (such as other seabirds, e.g., Shaffer *et al.*, 2006), it might be necessary to conduct this analysis on a truncated portion of the track where the looked-for change-point is likely to occur, or to enhance the model to account for the possibility of several change-points in the dataset.

Further research to understand why male eudyptid penguins are able to forgo 9 d of foraging at sea to return to land earlier than females, would require monitoring energetics at sea throughout the wintering period, possibly using heart rate recording (Green *et al.*, 2009).

Such data would help inform as to whether males are more efficient in the manner that they utilize their wintering areas. Indeed, male macaroni penguins tend to dive deeper than females during winter (Green *et al.*, 2005), which may confer male *Eudyptes* penguins a slightly higher potential foraging ability than females at that time.

Specializations in behavioural traits between males and females may lead to spatially and/or temporally skewed distribution of the individuals (Cook *et al.*, 2007; Catry *et al.*, 2012). Our results developped this theory further: behavioural correlates of sexes during the breeding season may indeed change an individuals' activity schedule well before breeding commences.

Acknowledgements

The Ethics Committee of IPEV approved the field procedure. The authors thank H. Maheo, M. Berlincourt, Q. Delorme, A. Knochel, R. Perdriat, J. Nezan, S. Mortreux, Y. Charbonnier and N. Mignot for their help in the field on the French Southern Territories, and A. Goarant for her help on analyses. The present work was supported financially and logistically by the ANR 07 Biodiv 'GLIDES', the Zone Atelier Antarctique (INSU-CNRS), the Institut Polaire Français Paul-Emile Victor (IPEV, programmes no. 394: resp. C.A. Bost, and 109: resp. H. Weimerskirch) and the Terres Australes et Antarctiques Françaises (T.A.A.F.) administration.

References

Authier, M., Martin, C., Ponchon, A., Steelandt, S., Bentaleb, I. & Guinet, C. (2012). Breaking the sticks: a hierarchical change-point model for estimating ontogenetic shifts with stable isotope data. Methods Ecol. Evol. 3, 281–290.

Bannasch, R., Wilson, R.P. & Culik, B. (1994). Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. J. Exp. Biol. 194, 83–96.

Bost, C.A., Clerquin, Y., Ropert-Coudert, Y. & Le Maho, Y. (2004). Exploitation of distant marginal ice zones by king penguins during winter. Mar. Ecol. Prog. Ser. 283, 293–297.

244 Bost, C.A., Thiebot, J.B., Pinaud, D., Cherel, Y. & Trathan, P.N. (2009). Where do penguins
245 go during the inter-breeding period? Using geolocation to track the winter dispersion of
246 the macaroni penguin. Biol. Lett. 5, 473–476.

247 Catry, T., Alves, J.A., Gill, J.A., Gunnarsson, T.G. & Granadeiro, J.P. (2012). Sex promotes
248 spatial and dietary segregation in a migratory shorebird during the non-breeding season.
249 PLoS ONE 7, e33811.

250 Cook, T.R., Cherel, Y., Bost, C.A. & Tremblay, Y. (2007). Chick-rearing Crozet shags
251 (*Phalacrocorax melanogenis*) display sex-specific foraging behaviour. Ant. Sci. 19, 55–
252 63.

253 Coulson, J.C. (2002). Colonial breeding in seabirds. In *Biology of marine birds*: 87–113.
254 Schreiber, E.A. & Burger, J. (Eds). Boca Raton: CRC Press.

255 Cribari-Neto, L. & Zeilis, A. (2010). Beta Regression in R. J. Stat. Softw. 34, 1–24.

256 Green, J.A., Boyd, I.L., Woakes, A.J., Warren, N.L. & Butler, P.J. (2005). Behavioural
257 flexibility during year-round foraging in macaroni penguins. Mar. Ecol. Prog. Ser. 296,
258 183–196.

259 Green, J.A., Boyd, I.L., Woakes, A.J., Warren, N.L. & Butler, P.J. (2009). Evaluating the
260 prudence of parents: daily energy expenditure throughout the annual cycle of a free-
261 ranging bird, the macaroni penguin *Eudyptes chrysolophus*. J. Avian Biol. 40, 529–538.

262 Hamer, K.C., Schreiber, E.A. & Burger, J. (2002). Breeding biology, life histories, and life
263 history-environment interactions in seabirds. In *Biology of Marine Birds*: 217–261.
264 Schreiber, E.A. & Burger, J. (Eds.). Boca Raton: CRC Press.

265 Hill, R.D. (1994). Theory of geolocation by light levels. In *Elephant seals: population*
266 *ecology, behavior, and physiology*: 227–236. Le Boeuf, B.J. & Laws, R.M. (Eds).
267 Berkeley: University of California Press.

268 Pütz, K., Raya Rey, A., Schiavini, A., Clausen, A.P. & Lüthi, B.H. (2006). Winter migration
269 of rockhopper penguins (*Eudyptes c. chrysocome*) breeding in the Southwest Atlantic: is
270 utilisation of different foraging areas reflected in opposing population trends? Polar Biol.
271 29, 735–744.

272 Pütz, K., Ingham, R.J., Smith, J.G. & Luthi, B.H. (2002). Winter dispersal of rockhopper
273 penguins *Eudyptes chrysocome* from the Falkland Islands and its implications for
274 conservation. Mar. Ecol. Prog. Ser. 240, 273–284.

275 R Development Core Team (2012). R: a language and environment for statistical computing.
276 R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

277 Raya Rey, A., Trathan, P. & Schiavini, A. (2007). Inter-annual variation in provisioning
278 behaviour of Southern Rockhopper Penguins *Eudyptes chrysocome chrysocome* at Staten
279 Island, Argentina. Ibis 149, 826–835.

280 Ropert-Coudert, Y., Kato, A., Poulin, N. & Gremillet, D. (2009). Leg-attached data loggers
281 do not modify the diving performances of a foot-propelled seabird. J. Zool. 279, 294–297.

282 Roth, T., Sprau, P., Naguib, M. & Amrhein, V. (2012) Sexually selected signaling in birds: A
283 case for Bayesian change-point analysis of behavioral routines. Auk 129, 660–669.

284 Shaffer, S.A., Tremblay, Y., Weimerskirch, H., Scott, D., Thompson, D.R., Sagar, P.M.,
285 Moller, H., Taylor, G.A., Foley, D.G., Block, B.A. & Costa, D.P. (2006). Migratory
286 shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer.
287 Proc. Natl Acad. Sci. USA 103, 12799–12802.

288 Shiomi, K., Yoda, K., Katsumata, N. & Sato, K. (2012) Temporal tuning of homeward flights
289 in seabirds. Anim. Behav. 83, 355–359.

290 Sorensen, M.C., Hipfner, J.M., Kyser, T.K. & Norris, D.R. (2009). Carry-over effects in a
291 Pacific seabird: stable isotope evidence that pre-breeding diet quality influences
292 reproductive success. J. Anim. Ecol. 78, 460–467.

293 Staniland, I.J., Robinson, S.L., Silk, J.R.D., Warren, N. & Trathan, P.N. (2012). Winter
294 distribution and haul-out behaviour of female Antarctic fur seals from South Georgia.
295 Mar. Biol. 159, 291–301.

296 Stahl, J.C., Derenne, P., Jouventin, P., Mougin, J.L., Teulières, L. & Weimerskirch, H.
297 (1985). Le cycle reproducteur des gorfous de l'archipel Crozet: *Eudyptes chrysolophus*, le
298 Gorfou macaroni, et *Eudyptes chrysocome*, le Gorfou sauteur. Oiseau Rev. Fr. Ornithol.
299 55, 27–43.

300 Sumner, M.D., Wotherspoon, S.J. & Hindell, M.A. (2009). Bayesian estimation of animal
301 movement from archival and satellite tags. PLoS ONE 4, e7324

302 Thiebot, J.B. & Pinaud, D. (2010). Quantitative method to estimate species habitat use from
303 light-based geolocation data. Endang. Species. Res. 10, 341–353.

304 Thiebot, J.B., Cherel, Y., Trathan, P.N. & Bost, C.A. (2011). Inter-population segregation in
305 the wintering areas of macaroni penguins. Mar. Ecol. Prog. Ser. 421, 279–290.

306 Thiebot, J.B., Cherel, Y., Trathan, P.N. & Bost, C.A. (2012). Coexistence of oceanic
307 predators on wintering areas explained by population-scale foraging segregation in space
308 or time. Ecology 93, 122–130.

309 Warham, J. (1975). The Crested Penguins. In *The biology of penguins*: 189–269. Stonehouse,
310 B. (Ed). London: Macmillan.

311 Williams, T.D. (1995). The Penguins. Oxford: Oxford University Press.

312 Wilson, R.P., Ducamp, J.J., Rees, G., Culik, B.M., & Niekamp, K. (1992). Estimation of
313 location: global coverage using light intensity. In *Wildlife telemetry: remote monitoring*
314 *and tracking of animals* 131–134. Priede, I.M. & Swift, S.M. (Eds.). Chichester: Ellis
315 Howard.

316 Wilson, R.P. & Vandenabeele, S.P. (2012). Technological innovation in archival tags used in
317 seabird research. Mar. Ecol. Prog. Ser. 451, 245–262.

318 Yamamoto, T., Takahashi, A., Yoda, K., Katsumata, N., Watanabe, S., Sato, K. & Trathan,
319 P.N. (2008). The lunar cycle affects at-sea behaviour in a pelagic seabird, the streaked
320 shearwater, *Calonectris leucomelas*. Anim. Behav. 76, 1647–1652.

321

Figure legends

Figure 1 Two examples (a, b) of a 'broken stick' determination process for homing decision date, based on the log-likelihood for existence of a change-point (upper panel) in the relative distance reached from the colony,at each location (lower panel): grey thick line shows the relative distance from the colony reached by the penguin, dashed black curve shows the beta regression fitted, and vertical dashed line shows the change-point inferred. The two examples shown refer to a male (a) and a female (b) *Eudyptes filholi* from Kerguelen; homing decision date was determined for location estimates no. 247, i.e. on 15/09/2007, and no. 279, i.e. on 28/09/2007, respectively.

Figure 2 'Bee swarm' plot showing the homing decision date inferred for each individual penguin surveyed in the different groups of species/locality/year available: A: *Eudyptes chrysolophus*, Crozet, 2007; B: *E. chrysolophus*, Kerguelen, 2006; C: *E. chrysolophus*, Kerguelen, 2007; D: *E. filholi*, Crozet, 2007; E: *E. filholi*, Kerguelen, 2007; F: *E. moseleyi*, Amsterdam, 2007.

338 **Table**

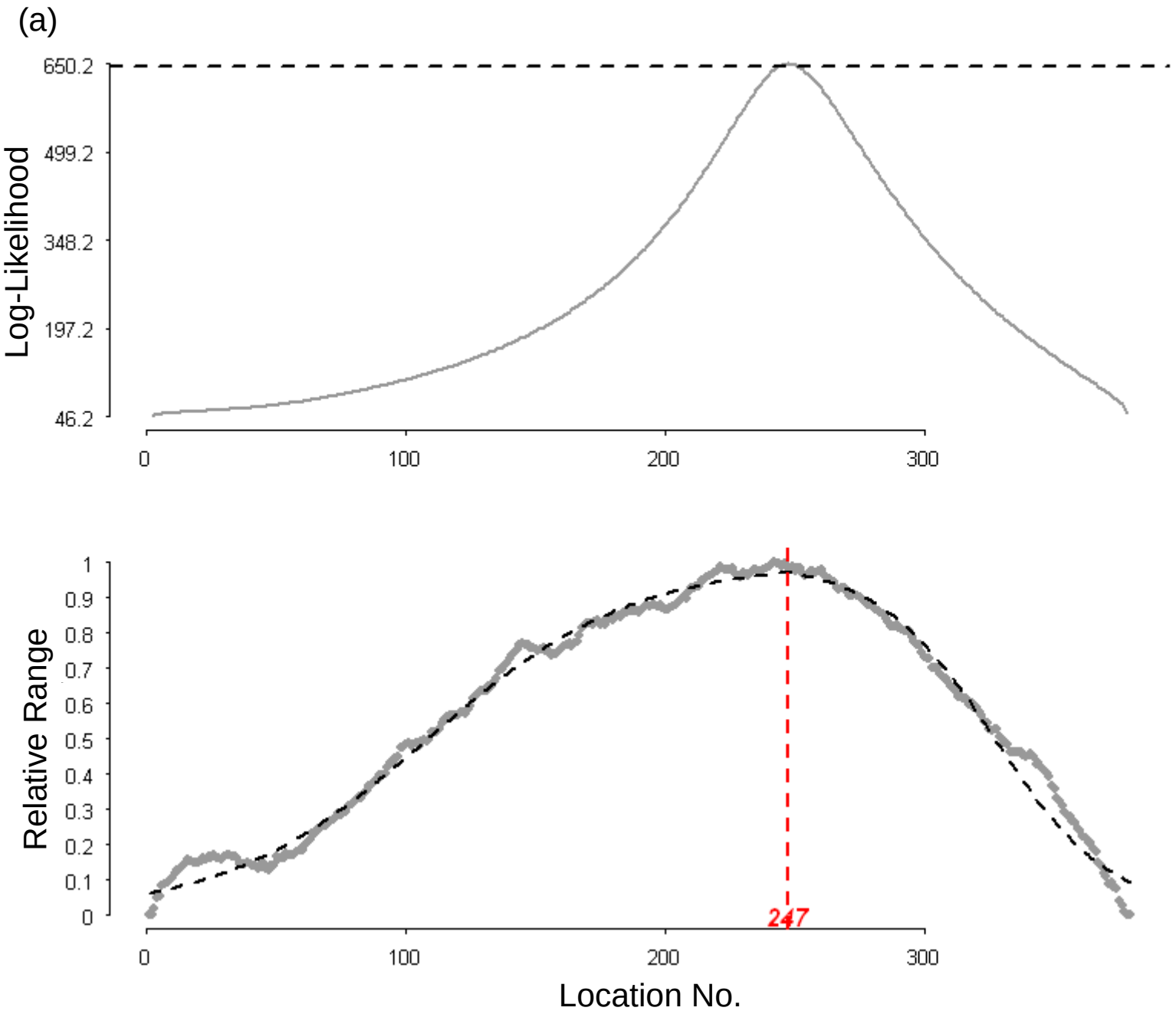
339

340 **Table 1** Summary of the penguin groups studied (species, locality, year and number of individuals of each sex), homing decision date (HD Date:
341 median ± standard deviation in d, format: dd/mm) and average 95% confidence interval width (CI: mean ± standard deviation in d) for male and
342 female penguins in each group surveyed during the inter-breeding period.

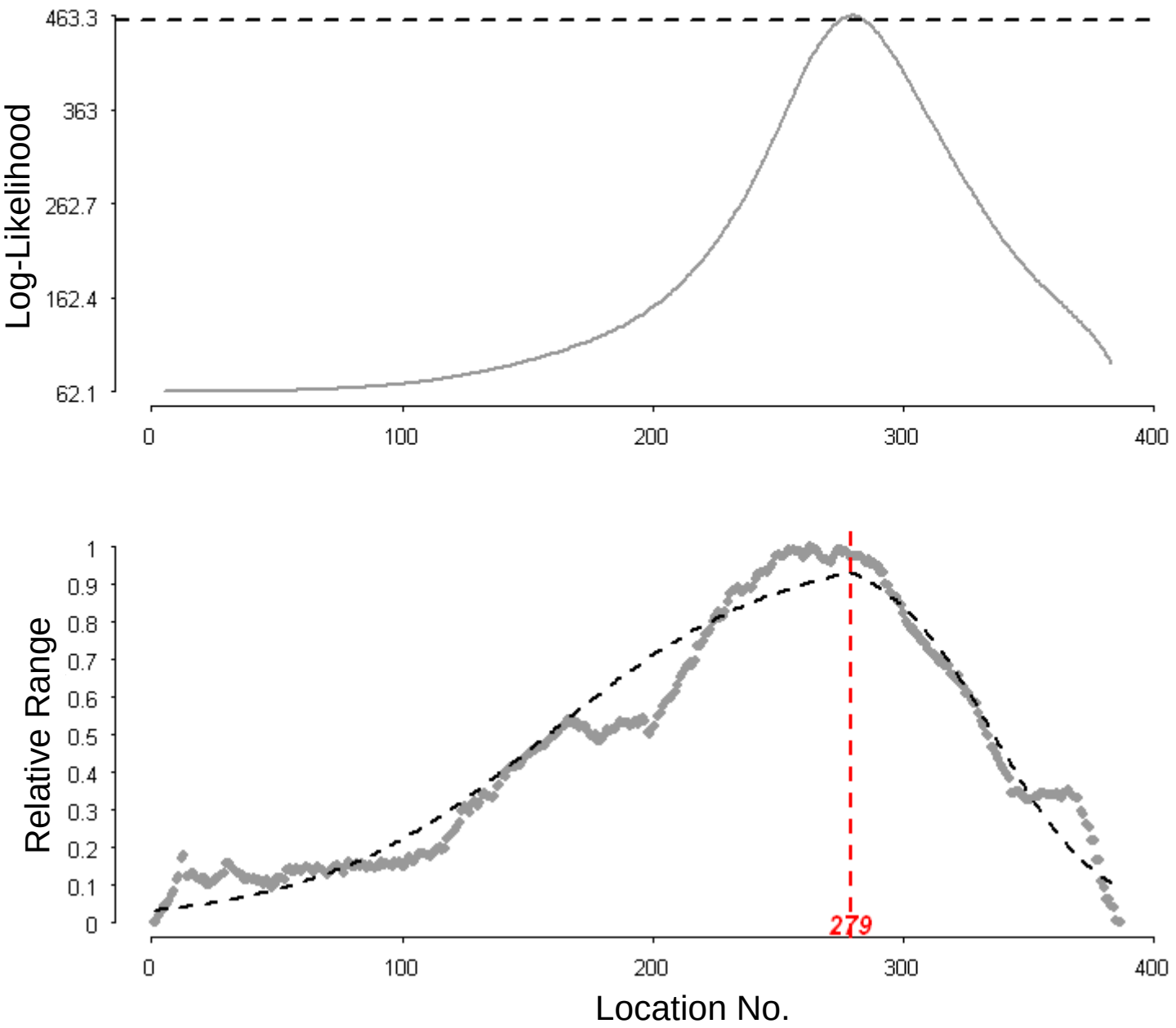
343

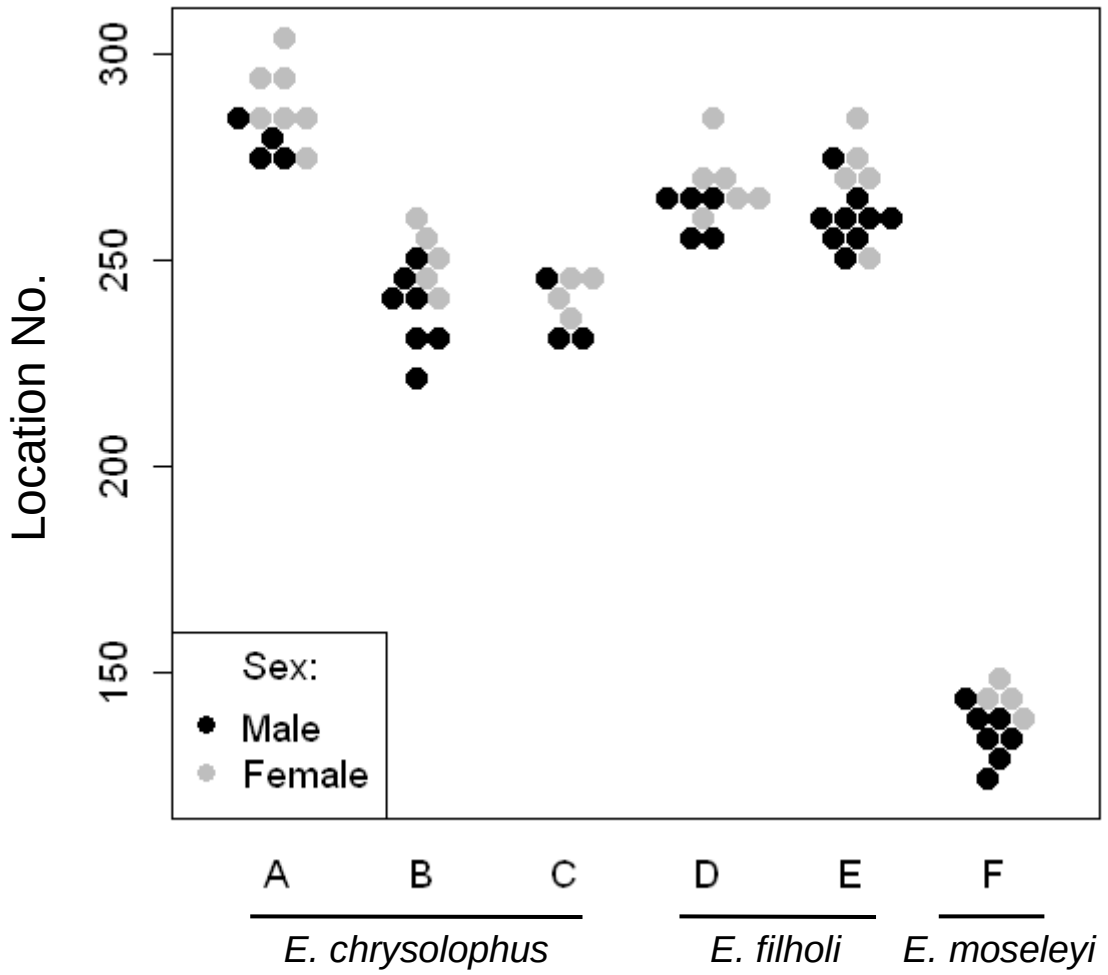
Species	Locality	Year	Males			Females		
			n	HD Date	95% CI	n	HD Date	95% CI
E. chrysolophus	Crozet	2007	4	04/10 ± 5.3	7.4 ± 4.1	7	12/10 ± 8.9	10.4 ± 5.8
	Kerguelen	2006	7	27/08 ± 10.8	6.6 ± 1.3	5	07/09 ± 7.4	7.2 ± 2.9
	Kerguelen	2007	3	21/08 ± 7.7	5.7 ± 1.2	4	02/09 ± 6.5	7.3 ± 1.3
E. filholi	Crozet	2007	5	22/09 ± 4.6	7.7 ± 3.1	6	26/09 ± 7.6	6.9 ± 2.4
	Kerguelen	2007	9	15/09 ± 7.1	5.4 ± 1.9	5	29/09 ± 12.9	5.5 ± 0.7
E. moseleyi	Amsterdam	2007	7	16/05 ± 6.5	5.8 ± 2.1	4	22/05 ± 3.8	5.6 ± 1.1

344


(a)
650.2
499.2
348.2
197.2
46.2
Log-Likelihood
0
100
200
300
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Relative Range
247
0
100
200
300
Location No.

(b)


463.3
363
262.7
162.4
62.1
Log-Likelihood
0
100
200
300
400
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Relative Range
279
Location No.


Location No.
300
250
200
150
Sex:
Male
Female
A
B
C
D
E
F
E. chrysolophus
E. filholi
E. moseleyi